THE FEEDING MECHANISMS AND PREFERRED FOODS OF THREE SPECIES OF PYCNOGONIDA

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By WILLIAM G. FRY

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SYNOPSIS

Laboratory experiments demonstrate that *Austrodecus glaciale* and *Rhynchothorax australis*, inhabiting the same Antarctic benthic environment, have highly specific and different food preferences. The structures of the proboscides and cephalic somites of the two species are adapted to these food preferences. *A. glaciale* is the first pycnogonid shown to feed on Polyzoa, while *Rh. australis* is adapted to feed on hydroid polyps. *Pycnogonum stearnsi*, from the north-eastern Pacific littoral, which feeds on Actinian tissue, is morphologically very similar to *Rh. australis*. The disposition of proboscis nerves and muscles in the three species is quite different from anything hitherto described in the Pycnogonida. In previous descriptions basal circular muscles have been interpreted as nerve rings. This prevented, up to now, the proposal of a mechanically reasonable interpretation of the functioning of the proboscis.

INTRODUCTION

Large areas of the sea bottom in McMurdo Sound (Ross Sea, Antarctica) are covered with a dense mat of sponge spicules. Within and on this mat occur large numbers

of coelenterates, polyzoans, echinoderms, sponges, lamellibranchs and polychaetes, and the interstices of the mat are largely filled with flocculent detritus. Bullivant (1959b, 1961) has published excellent photographs of this kind of environment.

Amongst other forms also present in varying abundance in this mat are several species of Pycnogonida, of which the most abundant appear to be *Austrodecus glaciale* Hodgson (s.s. Stock 1957) and *Rhynchothorax australis* Hodgson. Since the size ranges of these two species are very similar (Text-fig. 1), and since they were found in the same hauls on a number of occasions, it appears unlikely that they exploit equally all the aspects of their common environment.

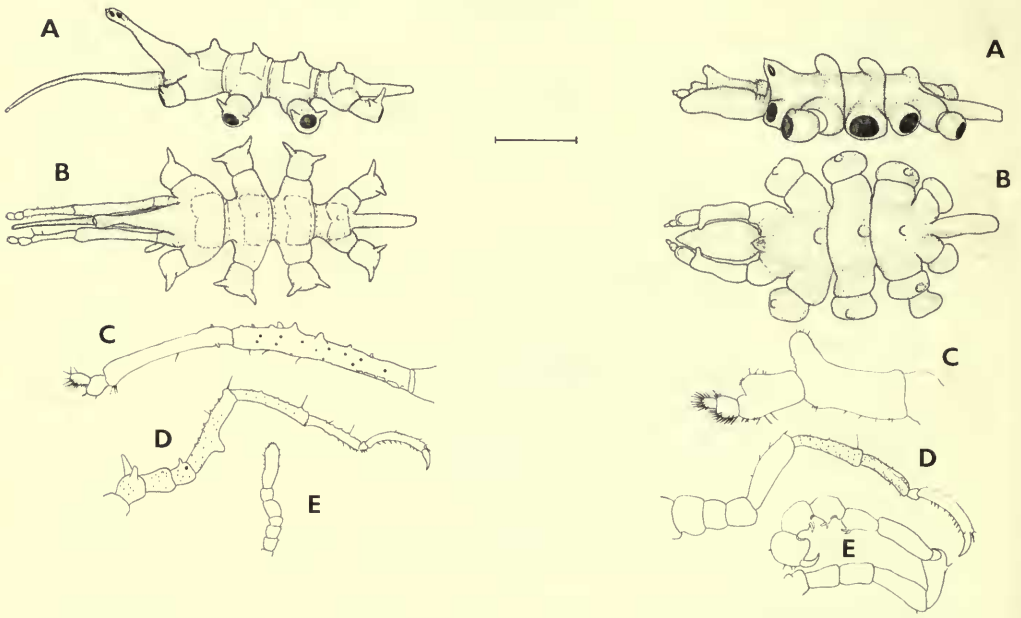

FIG. 1. Left : *Austrodecus glaciale* Hodgson. Right : *Rhynchothorax australis* Hodgson. A, view from left side ; B, dorsal view ; C, left palp ; D, 3rd left leg ; E, left oviger. A, B, and D to the scale indicated (1 mm.) ; C and E further enlarged.

During the austral summer of 1961/62, while the author was at the Naval Air Facility Base at McMurdo Sound, an attempt was made to determine the food preferences of *A. glaciale* and *Rh. australis* by studying their behaviour in an artificial environment in the laboratory. The observed differences in food preferences were sufficiently striking to warrant a detailed investigation of the morphology of the two species. The morphological differences between the two species are very marked, but since both species are adapted for life in a probably unique type of environment, it was felt advisable also to investigate the morphology of a species representative of a more ubiquitous environment.

Pycnogonum stearnsi Ives was available to the author in large numbers and was selected for comparison with the two Antarctic species. This species belongs to a genus with representatives in the littoral zone of most regions of the world. The

available information suggests that the preferred foods of all the species of the genus are various species of anthozoans. The faunal associations of *P. stearnsi* are—for a pycnogonid—very well documented.

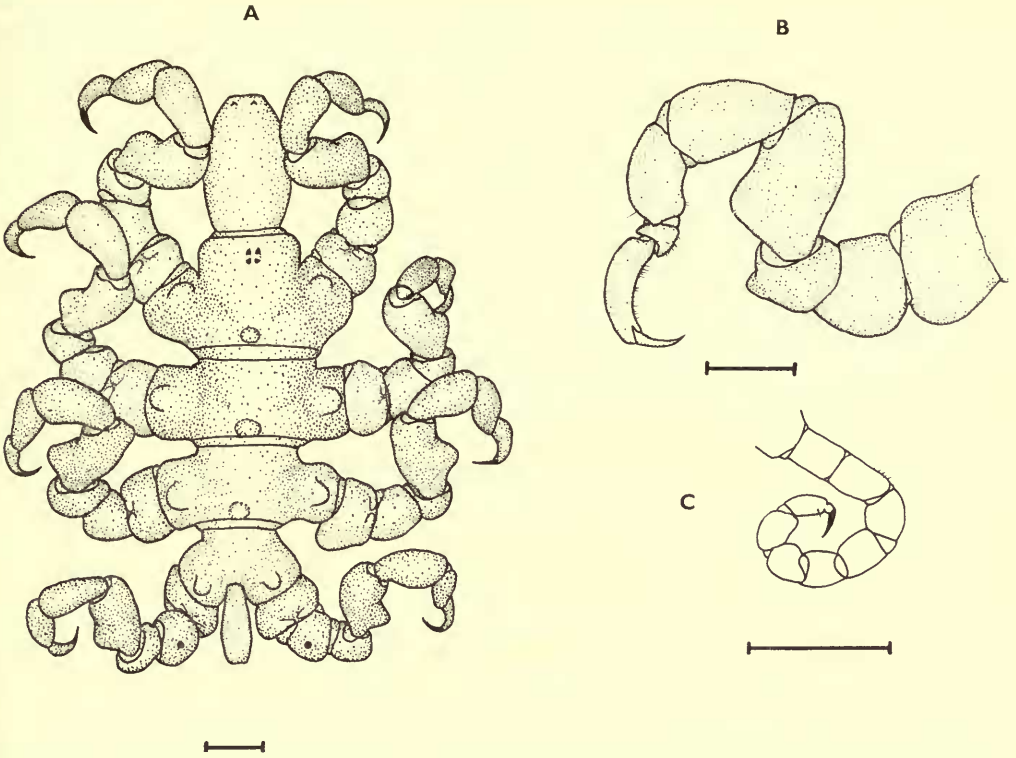

FIG. 2. *Pycnogonum stearnsi* Ives. A, dorsal view ; B, 3rd left leg ; C, left oviger of male. The scales represent 1 mm.

THE FEEDING PREFERENCES OF *AUSTRODECUS GLACIALE* AND *RHYNCHOTHORAX AUSTRALIS*

Material

The specimens of Pycnogonida, together with other organisms and substrate from their immediate environment, were collected with modified Petersen and orange-peel grabs worked through the ice-holes maintained by the Stanford University laboratory personnel. *A. glaciale* and *Rh. australis* proved to be most plentiful under Ice Hole No. 3, situated at 77° 59′ 5″ S., 166° 44′ 3″ E., in approximately 280 metres of water. The Pycnogonida retained for observation and subsequent histological work were all taken at this station during November.

Potential food organisms were selected from the samples which contained specimens of the two species of pycnogonids. The range of potential food was further narrowed, to what appeared to be sixteen species, by the selection of only those kinds of material on which pycnogonids had been observed during the sorting of the contents of 24 grab hauls from Ice Hole No. 3. Subsequent systematic evaluation

revealed that in fact 18 species of Coelenterata, Polyzoa, Tunicata, and Porifera were used in the study. Table 1 lists the taxa and the symbols by which they are referred to below.

TABLE I

Taxonomic status of the sixteen kinds of potential food material presented to *Rhynchothorax australis* and *Austrodecus glaciale*.

Coelenterates.

Eudendrium tottoni Stechow = Hy 1.[1]
Symplectoscyphus epizooticus Totton = Hy 2.
Symplectoscyphus vanhoeffeni Totton = Hy 3.
Thouarella variabilis Wright & Studer = Hy 4.
Alcyonium paessleri May = Hy 5.
Hydrodendron arborea (Allman) = Hy 6.

Polyzoa.

Cellarinella laytoni Rogick = Br 1.
Escharoides bubeccata Rogick + *Notoplites drygalski* (Kluge) = Br 2.
Cellarinella foveolata (Waters)[2] = Br 3.
Camptoplites bicornis (Busk) var. *magna* (Kluge) + *Cellaria wandeli* Calvet = Br 4.
Cellaria vitrimuralis Rogick + *C. moniliorata* Rogick = Br 5.

Tunicate.

Unidentified = Tu 1.

Porifera.

Suberites sp. = Sp 1.
Cinachyra barbata Sollas = Sp 3.
Tedania sp. = Sp 4.
Suberites sp. = Sp 7 (= Sp 1).

[1]The letters and numbers after the names correspond to the potential food materials listed in Tables II and III.

[2]Possibly a synonym of both *C. roydsi* Rogick and *C. rossi* Rogick.

Maintenance of the Organisms

Grab contents were sorted in the laboratory, in trays jacketed with fresh snow, and the pycnogonids and potential food materials were placed in shallow jars of fresh sea water at −1·8°C. The jars were kept in a large cooling unit. During fifteen sets of observations, the water temperature was observed to fluctuate between −0·5 and −1·8°C. The organisms appeared unaffected by these fluctuations. The pycnogonids remained active throughout the whole period of study, and the coelenterates maintained rapid reactions to gentle probing.

The sea water in the jars was replaced with equal quantities of fresh sea water every 48 hours, and the potential food organisms were replaced with freshly collected material every 96 hours.

The Pycnogonida were segregated according to species, and each jar of pycnogonids contained fragments of each of the sixteen kinds of food material. Care was taken to ensure that the quantities of each of the potential food materials in each jar were as nearly equal as possible. When several very small fragments of any one kind of food material were required to make up the correct total bulk of that material, the small fragments were placed together. It was hoped that these precautions would ensure that the chances of a pycnogonid encountering any one kind of food material, during random locomotion, would be equal for all the kinds of food material.

An additional precaution taken was to ensure that only potential food material which was mostly or entirely composed of live tissues was presented to the pycnogonids.

Observations

Observations were made over a period of nine days, at eight or twelve hour intervals. A count was made, at each set of observations, of the number of specimens of each species of pycnogonid on each kind of potential food material. During the periods of observation, the jars of organisms were kept jacketed in fresh snow, and studied with the aid of a binocular microscope. Great care was taken to avoid disturbing the contents of the jars while the counts were made.

Specimens of *Rh. australis* were seen to ingest polyps of *Eudendrium tottoni* but ingestion of food by *A. glaciale* was never observed. However, a check was made, at each set of observations, on the degree of distension of the gut in all of the pycnogonids. This is readily done as, during life, both species of pycnogonid are sufficiently transparent for the gut to be visible. Throughout the nine days of observations all the pycnogonids maintained full, or partially full, gut diverticula.

Data

The results of observations on seventeen specimens of *Rh. australis* and five specimens of *A. glaciale* are shown in Table II and III.

TABLE II

The observed frequencies of occurrence of five adult specimens of *Austrodecus glaciale* Hodgson on sixteen kinds of potential food material during a period of nine days.

	1st Presentation		*2nd Presentation*		*Total*	
	f	%f	f	%f	f	%f
Hy 1	4	13·76	1	3·44	5	8·60
Hy 2	2	6·88	2	6·88	4	6·88
Hy 3	1	3·44	0	0·0	1	3·72
Hy 4	0	0·0	0	0·0	0	0·0
Hy 5	0	0·0	0	0·0	0	0·0
Hy 6	0	0·0	1	3·44	1	1·72
Br 1	1	3·44	1	3·44	2	3·44
Br 2	2	6·88	3	10·32	5	8·60
Br 3	8	27·52	10	34·40	18	30·96
Br 4	4	13·76	1	3·44	5	8·60
Br 5	0	0·0	1	3·44	1	1·72
Tu 1	0	0·0	1	3·44	1	1·72
Sp 1	0	0·0	0	0·0	0	0·0
Sp 3	3	10·32	4	13·76	7	12·04
Sp 4	3	10·32	0	0·0	3	5·16
Sp 7	1	3·44	4	13·76	5	8·60
Totals	29		29		58	

TABLE III

The observed frequencies of occurrence of seventeen adult specimens of *Rhynchothorax australis* Hodgson on sixteen kinds of potential food material during a period of nine days.

	1st Presentation		*2nd Presentation*		*Total*	
	f	%f	f	%f	f	%f
Hy 1	42	45·78	15	15·75	57	30·76
Hy 2	3	3·27	6	6·30	9	4·78
Hy 3	0	0·0	7	7·35	7	3·67
Hy 4	2	2·18	7	7·35	9	4·76
Hy 5	0	0·0	4	4·20	4	2·10
Hy 6	0	0·0	5	5·25	5	2·62
Br 1	0	0·0	4	4·20	4	2·10
Br 2	3	3·27	8	8·40	11	5·83
Br 3	6	6·54	4	4·20	10	5·37
Br 4	1	1·09	5	5·25	6	3·17
Br 5	3	3·27	5	5·25	8	4·26
Tu 1	0	0·0	1	1·05	1	0·52
Sp 1	13	14·27	2	2·10	15	8·28
Sp 3	7	7·63	3	3·15	10	5·39
Sp 4	5	5·25	15	15·75	20	10·60
Sp 7	6	6·54	4	4·20	10	5·37
Totals	91		95		186	

These data were analysed by means of the χ^2 test, in order to ascertain how far the segregation of the pycnogonids on the potential food organisms differed from situations due entirely to chance wandering. The null hypothesis proposed for the χ^2 test was that the pycnogonids had no preference for any particular kind of animal substrate, and that they would therefore be expected to distribute themselves equally among the sixteen kinds of potential food material. This hypotheses was strongly discredited for both *Rh. australis* and *A. glaciale*, since for both sets of data $P = \gg 0{\cdot}001$.

From this result of χ^2 tests it is clear that, within the experimental environments at least, *Rh. australis* has a strong preference for association with the hydroid *Eudendrium tottoni* Stechow (= Hy 1), and that *A. glaciale* has a strong preference for association with the polyzoan *Cellarinella foveolata* (Waters) (=Br 3). In the case of both pycnogonids these major preferences appear to be three times as strong as the animals' preference for association with any other kind of potential food.

Although details of the feeding mechanisms of the two species of pycnogonid and the morphologies of the preferred food substances strongly suggest that the calculated preferences are strongly associated with quite different feeding mechanisms (see below), the effect of a large part of the experimental environment cannot be determined accurately. This is the free space in the experimental containers.

Both *A. glaciale* and *Rh. australis* show very marked thigmotropism when disturbed. Individuals will cling tightly together if placed in water on a bare smooth surface. The high percentage of total occurrences on potential food materials and the corresponding low percentage of occurrences free in the containers is probably a good indication of the strength of this thigmotropism.

Frequencies on Food Materials	*Rhynchothorax*	*Austrodecus*
Total Possible	216 = 100%	64 = 100%
Total Observed	186 = 85·96%	58 = 90·59%

It is quite possible that thigmotropism induced artificially high frequencies of occurrences on all the potential food materials, since the experimental substrate—smooth floored glass jars—was very far removed in texture from the pycnogonids' natural substrate of sponge spicules, hydroids, flocculent detritus, etc.

The total of 10–15% of non-occurrences on potential food substances indicates that thigmotropism was not the only factor controlling the distribution of the pycnogonids within the jars.

THE FOOD PREFERENCES OF PYCNOGONUM STEARNSI

The faunal associations of this species are so well documented (Hedgpeth 1951, Ricketts & Calvin 1963, Zeigler 1960), and apparently so consistent, that no experimental determination of food preferences seems necessary. *P. stearnsi* occurs in the mid-tide and low-tide horizons of the littoral zone along the western coast of North America from Alaska to Southern California (Hedgpeth 1961). It has been found closely associated with hydroids (e.g. *Aglaophenia* spp.), the tunicate *Clavelina huntsmani*, and, by far the most frequently, with the anemones *Anthopleura xanthogrammica* (Brandt) and *Bunodactis elegantissima* (Brandt).* The pycnogonids are frequently found clustered around the bases of the anemones, with their proboscides clearly inserted into the anemones' tissues. The author has found immature nematocysts amongst the gut contents of specimens of *P. stearnsi*, freshly collected from round the bases of both species of anemone. There can thus be little doubt that the anemones form an important part of the food of this species.

THE MORPHOLOGY OF THE PROBOSCIS IN THE THREE SPECIES

Methods

All specimens of the three species were treated in the same fashion, preparatory to examination. Before fixing in Bouin's solution, the specimens were narcotised, by adding ethyl acetate to the water in which they were resting. It was hoped that this would bring about the relaxation of all muscles. Immersion of active pycnogonids in formalin or alcohol frequently results in violent spasmodic movements, and the animals may remain in spasm until the tissues are fixed. The possibility that muscles may be found in a state of violent, abnormal, contraction, renders even more difficult than usual the interpretation of mechanical systems by means of serial sections alone.

Prior to sectioning, the animals† were immersed in formal formic acid. Without this precaution, even if specimens are mounted in ester-wax for sectioning, it is very difficult to obtain whole sections. The pycnogonid cuticle is not only very thick, but

*It appears likely that these two anemones are but form varieties of a single species.

†B.M. (N.H.) Regn. Nos. 1963.6.27.1–5 and 1964.1.13.1–4.

very brittle. Even following immersion in the acid solution and sectioning in ester-wax, it was not possible to obtain entire sections thinner than 10μ, and to obtain useful sections of the largest specimens of *P. stearnsi* it was necessary to treat them with diaphanol.

All sections were stained with Mallory's triple stain. This stain was selected because its effects on cuticle with different mechanical properties appear to be remarkably constant. There is striking similarity in the distribution of stain colours in the cuticles of young and old specimens of all three species. The distribution of colours in the stained cuticles of the three species of pycnogonids is quite reconcilable with the associations of colour and mechanical properties described by Manton (1958, pp. 548–550).

The extrinsic musculature of the proboscis.

In outward appearance the pycnogonid proboscis is a simple tube, which varies in its external diameter at different points along its length. Morphological studies show clearly that the underlying plan of symmetry of the proboscis is triradial, and this is in fact suggested in external appearance by the presence of three lip lobes.

Seen in cross-section, the proboscis appears to have been formed by the fusion of a single dorsal and two ventrolateral antimeres. (See Text-figs. 6 and 7, Pl. 3–5.) Embryological studies, culminating in the recent publication by Sanchez(1959), indicate that the dorsal antimere is an outgrowth from a " cephalic " somite, while the two ventrolateral antimeres arise from a slightly more posterior somite. Some circumstantial evidence in support of this explanation of the origin of the ventrolateral antimeres occurs in the genera *Phoxichilidium* and *Anoplodactylus*, in which the proboscis frequently bears a pair of ventrolateral protuberances. These outgrowths indicate that the somite giving rise to the ventrolateral antimeres of the proboscis may, in the past, have borne a pair of ventral appendages.*

While the intrinsic musculature, the gut configuration, and the nervous system of the proboscis are clearly based on a triradial plan of symmetry, the muscles causing the entire proboscis to move are not disposed triradially. The extrinsic muscles consist of at least two pairs of major muscles, which may be subdivided to some extent, and one smaller pair of ventral muscles which are variably present.

One of the major pairs of muscles retracts the dorsal proximal end of the proboscis. This pair of muscles is referred to here as the " M 1 muscles " (Text-figs. 3, 4 and 5, Pl. 1. M 1). The other major pair of muscles retracts the ventral proximal end of the proboscis. This pair is referred to here as the " M 2 muscles " (Text-figs. 3, 4 and 5, Pl. 1. M 2), while the " M 3 muscles " (Text-fig. 3, M 3) are the smaller muscles which appear to be partly ancillary in function to the M 2 muscles. Other muscle pairs not directly concerned in the movements of the proboscis are referred to as " M 4 ", " M 5 " (Text-figs. 3, 4 and 5).

In *Rhynchothorax australis* (Text-fig. 3) three pairs of extrinsic muscles appear to be concerned in movements of the proboscis.

The muscles of the pair M 1 have their origins, on a transverse dorsal apophysis

*Stock (1963) has described a new species, *Anoplodactylus unilobus*, in which the proboscis bears a single ventral outgrowth.

(Ap 1), medial to the origins of the M 2 muscles. The M 1 muscles pass forward between the dorsal ganglion and the dorsal surface of the gut, within the circumoesophageal commissure, and insert on the anterior dorsal surface of the arthrodial membrane between the proboscis and the cephalic somite. In their passage forward, the two muscles converge, so that they are inserted on the arthrodial membrane more closely than they originate on the wall of the cephalic somite.

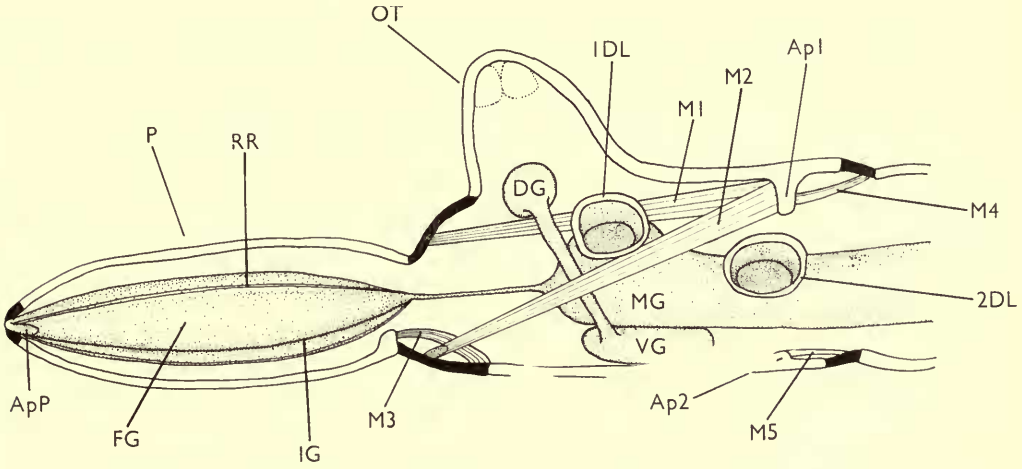

FIG. 3. Proboscis and cephalic somite of *Rh. australis* seen in diagrammatic longitudinal optical section. Unsclerotized arthrodial membrane is shown as solid black. Only the structures of the left side are shown. See p. 223 for the key to the lettering.

The M 2 muscles have their origins, on the same dorsal transverse apophysis (Ap 1), lateral to the origins of the M 1 muscles. They pass forward and downward, outside the circumoesophageal commissure, and are inserted on the ventrolateral walls of the arthrodial membrane between proboscis and cephalic somite. In their forward passage the two muscles of the pair diverge slightly.

The M 3 muscles are very much shorter and less stout than either the M 1 or the M 2 muscles. They have their origins on the proximal ventral portion of the arthrodial membrane between proboscis and cephalic somite, and their insertions on a low apophysis on the ventral proximal edge of the proboscis wall.

In this species, as in the other two studied, there are no visible antagonists to these sets of muscles, and it is reasonable to suppose that the fluid body contents are the antagonists of all the extrinsic proboscis muscles.

Accepting this hypothesis, and using it to interpret the mechanics of proboscis movement, it may be said that, during life the system is in balance when all the extrinsic muscles have slight tonus, and the proboscis is held with its longitudinal axis roughly parallel to the longitudinal axis of the body. When the M 1 muscles contract, the proximal dorsal surface of the proboscis will be pulled back and the dorsal portion of the arthrodial membrane will buckle inwards. The whole proboscis

will tilt about an axis at the line of folding in the arthrodial membrane and in this way the distal end of the proboscis will be raised slightly.

When the M 2 muscles contract the ventral proximal edge of the proboscis will be pulled backwards and upwards. The net effect of this movement will be a lowering of the distal end of the proboscis.

The angles which the M 1 and M 2 muscles make with the longitudinal axes of the body and proboscis suggest that the M 2 muscles will produce a much greater movement from the balanced state than will the M 1 muscles.

It appears that the M 1 muscles have three functions. When acting by themselves, they will assist the hydrostatic pressure in returning the system to the balanced state, when the M 2 muscles relax after a major contraction. When the M 1 and the M 2 muscles are contracted slightly, the balance of the system will be maintained, and when the M 1 and M 2 muscles are both strongly contracted, the whole proboscis will be slightly retracted.

The divergence of the M 2 muscles suggests that they are capable of producing slight lateral movements of the base of the proboscis—and hence of its distal end—when one or other of them contracts alone.

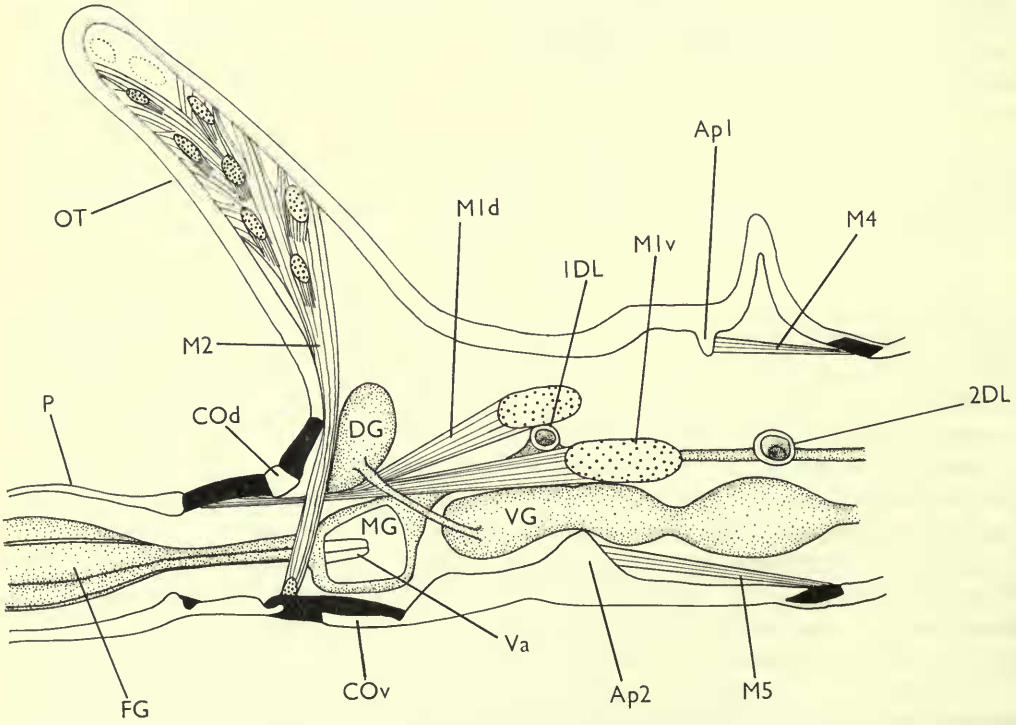

FIG. 4. Cephalic somite and proximal portion of the proboscis of *A. glaciale* seen in diagrammatic longitudinal optical section. Unsclerotized arthrodial membrane is shown as solid black. Only the structures of the left side are shown, except where portion of the midgut wall has been cut away to reveal the valve (Va) between fore- and midguts. See p. 223 for the key to the lettering.

In *Austrodecus glaciale* (Text-fig. 4) only two pairs of muscles are involved in moving the proboscis, but the region of articulation between proboscis and cephalic somite is more complicated than in either *Rh. australis* or *Pycnogonum stearnsi*.

The arthrodial region between proboscis and cephalic somite consists of two areas of unsclerotised membrane, separated by a collar of highly sclerotized cuticle (Text-fig. 4, Pl. 1. CO d and CO v). The proximal area of membrane is not continuous over the whole circumference of the joint, for the wide, ventral, portion of the sclerotized collar is continuous, through a thin layer of highly sclerotized cuticle, with the thick, red-staining, wall of the cephalic somite. The distal area of membrane is continuous over the whole circumference of the joint, forming a ring.

The M 1 muscles each have two areas of origin (M1 d and M1 v) on the lateral walls of the cephalic somite. The two portions of each muscle pass forward and merge almost immediately beneath the dorsal ganglion. The muscles then pass through the circumoesophageal commissure, through the sclerotized collar in the articulation, and insert on the arthrodial membrane immediately behind the dorsal proximal edge of the proboscis. During their passage forward the muscles converge.

The M 2 muscles are much more massive than the M 1 muscles. They have their origins over all the wall of the ocular tubercle, which is enormously elongated in this species. They pass almost straight downwards, outside the circumoesophageal commissure, and insert on the ventrolateral walls of the arthrodial membrane, immediately posterior to the proximal edge of the proboscis.

If anything, the difference in height between the origins and insertions of the M 1 muscles, and the angles that they made with the longitudinal axis of the trunk and proboscis, are less than in *Rh. australis*. But contraction of the M 1 muscles will produce strong tension forces in the anterior dorsal portion of the arthrodial membrane. Part of the force will be spent in causing that portion of the membrane to buckle inwards and slightly down, and part in making the sclerotized collar tilt about its posterior basal union with the floor of the cephalic somite. This will not only pull backwards the dorsal proximal edge of the proboscis, cause the whole proboscis to tilt about an axis in the plane of flexure of the arthrodial membrane, and thereby raise the tip of the proboscis, but will also cause slight raising of the whole proboscis.

The positions and shapes of the regions of arthrodial membrane and the collar provide two ventral hinges, about which the proboscis may tilt. The posterior hinge (the thin, sclerotized, cuticle joining the collar and cephalic somite) will allow the collar to tilt backwards only under the forces exerted by the M 1 muscles ; being very highly sclerotized, it will be highly elastic, and therefore considerable force will have to be generated around the hinge if the proboscis is to tilt about an axis in the plane of the hinge. The M 1 muscles are disposed so that their contraction will cause movement about the elastic hinge region with relatively little expenditure of energy. All but the most violent contractions of the M 2 muscles, on the other hand, will cause no movement about this elastic hinge region. The almost vertical direction of pull of the M 2 muscles will cause movement about the second hinge region—the anterior ventral portion of the arthrodial membrane.

Resolution of the forces exerted by the M 2 muscles in the joint between proboscis and cephalic somite shows that the major part of the forces will tend to raise the ventral proximal end of the proboscis, while only a very small component will tend to rotate the collar. It appears that the elasticity of the posterior ventral hinge region will safely counteract this small component, with the result that the proximal ventral edge of the proboscis will be tucked up inside the anterior ring of arthrodial membrane. Such a movement will cause the tip of the proboscis to be thrust downwards.

The size of the M 2 muscles in this species suggests that the tip of the proboscis can be moved ventrally with considerable force. Such a supposition agrees well with the suggested method of feeding described below (see p. 217).

The disposition of the muscles in this species does not suggest that the whole proboscis can be retracted, and in fact retraction of a strongly downcurved proboscis does not appear to be a very useful movement.

Pycnogonum stearnsi (Text-fig. 5) is similar to *A. glaciale* in that only two pairs of muscles are involved in moving the proboscis, and is similar to *Rh. australis* in possessing no sclerotized collar in the region of articulation, but is quite unlike either species in that the M 1 muscles do not pass through the circumoesophageal commissure.

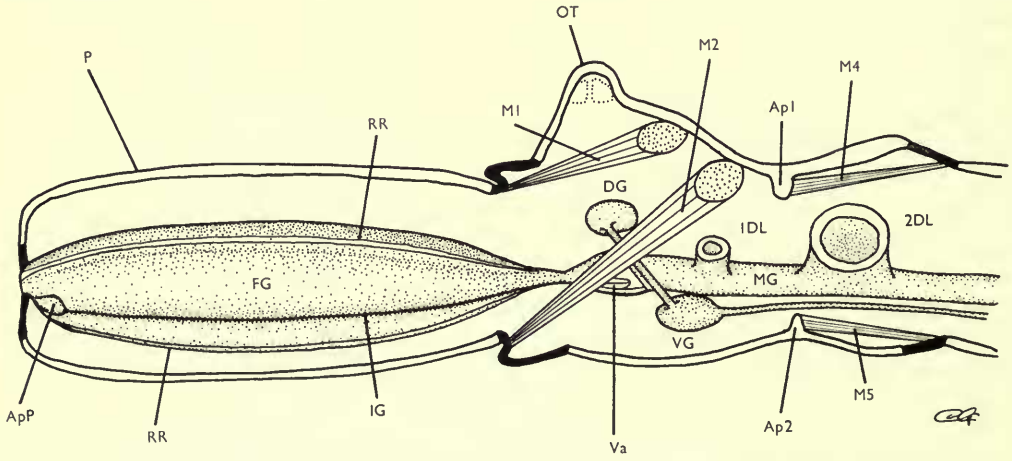

Fig. 5. Diagrammatic longitudinal optical section of the cephalic somite and proboscis of *P. stearnsi*. Unsclerotized arthrodial membrane is shown as solid black. Only structures of the left side are shown, except where a portion of the midgut wall has been removed to show the valve (Va) between midgut and foregut. See p. 223 for the key to the lettering.

The M 1 muscles have their origins on the dorsal wall of the cephalic somite, partly inside the ocular tubercle. They pass downwards and forwards immediately dorsal to the dorsal ganglion, and insert on the distal dorsal edge of the arthrodial membrane between proboscis and cephalic somite.

The M 2 muscles have their origins on the lateral walls of the cephalic somite, posterior to the regions of origin of the M 1 muscles. They pass forward and down-

ward, outside the circumoesophageal commissure and insert on the ventrolateral walls of the arthrodial membrane.

As in the other species, the raising and lowering of the tip of the proboscis appears to be brought about by contraction of the M 1 and M 2 muscles respectively. As in *Rh. australis*, the relatively small angles which the muscles make with the longitudinal axis of the body suggest that the vertical movements of the proboscis are unlikely to be very powerful.

Contraction of both M 1 and M 2 muscles together will tend to retract the whole proboscis, and it seems reasonable to suppose that the proboscis is retracted during feeding movements. Unlike the situation in *A. glaciale*, where the proboscis is strongly downcurved, it appears that retraction of a straight proboscis, from massive, soft, food material, is a useful movement.

Taxonomic significance of the disposition of the extrinsic muscles.

While the internal structures of the proboscis have been the subject of several studies, the nature and disposition of the extrinsic proboscis musculature has received very little attention.

Dohrn (1881) was the first to illustrate the musculature, but his figures suggest that he could not interpret with any certainty the structures that he observed. This is doubtless due to the fact that he examined his specimens as solid, transparent, objects, and neither sectioned nor dissected them. Hoek (1881) appears to be the only other author to describe or illustrate the extrinsic musculature of the proboscis,* and while his figure of the transverse sectional appearance of the cephalic somite of *Colossendeis leptorhynchus* Hoek (Pl. 18, fig. 7) is in some respects more informative of the disposition of proboscis muscles than the figures by Dohrn, it gives no indication of the sites of origin and insertion of muscles. Neither of these authors discusses the extrinsic proboscis musculature other than by way of a passing reference in the text.

Dohrn (loc. cit.) illustrated part or all of the extrinsic musculature of *Ascorhynchus* (= *Barana*) *castelli* Dohrn, *Achelia echinata* Hodge (= *Ammothea fibulifera* Dohrn), and *Achelia* (= *Ammothea*) *langi* Dohrn. According to the figures in all three species the muscles retracting the upper surface of the proboscis (= M 1 muscles) originate on the dorsal wall of the cephalic somite, behind the ocular tubercle. In *A. castelli* and *Ach. echinata* the M 1 muscles consist of a single pair, which passes forward through the circumoesophageal commissure to its insertions on the dorsal edge of the proboscis. In *Ach. langi* (Dohrn, 1881, Pl. 5, fig. 4), on the other hand, the M 1 muscles consist of two pairs, and while the member of each pair with the more ventral origin in the wall of the cephalic somite runs forward through the circumoesophageal commissure, the member of the pair of more dorsal origin runs over and in front of the dorsal ganglion. Thus, while in *Rh. australis* the members of each pair of M 1 muscles meet posterior and ventral to the dorsal ganglion, in *Achelia langi* they meet anterior and dorsal to the dorsal ganglion.

Dohrn's figures of *Ascorhynchus castelli* (1881, Pl. 1, fig. 2) indicates that the muscles retracting the base of the proboscis (= M 2 muscles) originate inside the

*Helfer & Schlottke (1935) simply reproduce Dohrn's figure of *A. castelli*, and do not comment on it.

anterior surface of the ocular tubercle, and under the cephalic lobes. This condition is very similar to that observed in *Austrodecus glaciale*.

It is apparent that the proboscis of most, if not all, the species of *Ascorhynchus* is highly mobile in a vertical plane, and can be moved so as to lie almost parallel with the trunk. It is not surprising, therefore, to find that the M 2 muscles follow the same course as they do in *A. glaciale*, although in the latter species the muscles appear to produce small movements of great power, instead of larger movements.

Dohrn's figure of *Achelia fibulifera* gives no indication of the disposition of the M 2 muscles in this species, but his illustration of *Ach. langi* suggests that here the M 2 muscles originate on the dorso-lateral surface of the cephalic somite.

Hoek's illustration of the cephalic somite of *Colossendeis leptorhynchus* (1881, Pl. 18, fig. 7) shows clearly the passage of the M 1 muscles through the circum-oesophageal commissure, while the level in the cephalic somite at which the section was made indicates that the M 2 muscles also have their origins on the dorsal wall of the cephalic somite, posterior to the ocular tubercle.

From amongst all the Pycnogonida there is information on the nature of the extrinsic proboscis musculature of only six species. These six species are drawn from five genera which have long been considered very distinct, on the grounds of their external morphology. It is, therefore, no surprise to find that, in general, the dispositions of the extrinsic proboscis muscles differ widely amongst the five genera. Two points are worthy of remark. The first is the striking dissimilarity between two species of the same, long established, genus, (*Achelia echinata* and *Ach. langi*), and the second is the similarity between *Rhynchothorax australis*, *Achelia echinata*, and *Colossendeis leptorhynchus*, which are members of three long separated genera.

Previous interpretations of the Morphology of the Proboscis.

Longitudinal, transverse, and horizontal sections of the three species reveal that not one of the previous interpretations of the structure and functioning of the proboscis is entirely adequate.

The structure of the proboscis was first elucidated by Dohrn (1881) for *Trygaeus communis* Dohrn, and for *Phoxichilus vulgaris* Dohrn and *Ph. charybdaeus* Dohrn (both = *Endeis spinosa* Montagu). Hoek (1881) examined the structures in the proboscis of *Nymphon robustum* Bell and Wirén (1918), in his discussion of the morphology and phylogeny of the Pycnogonida, gave a highly detailed description of the nervous system of the proboscis of *Nymphon brevirostre* Hodge.

The only other author to discuss in detail the structures within the pycnogonid proboscis has been Henry (1953), who did not concern herself with musculature.

The structures which Dohrn and Hoek claim to have found in the species that they studied are shown in Text-fig. 6.

The Alimentary Canal.

The cavity of the alimentary canal within the proboscis is lined with cuticle, which is continuous anteriorly with the outer cuticle of the proboscis. No tissues have ever been described as occurring inside this cuticular wall, although it is lost and renewed at ecdysis.

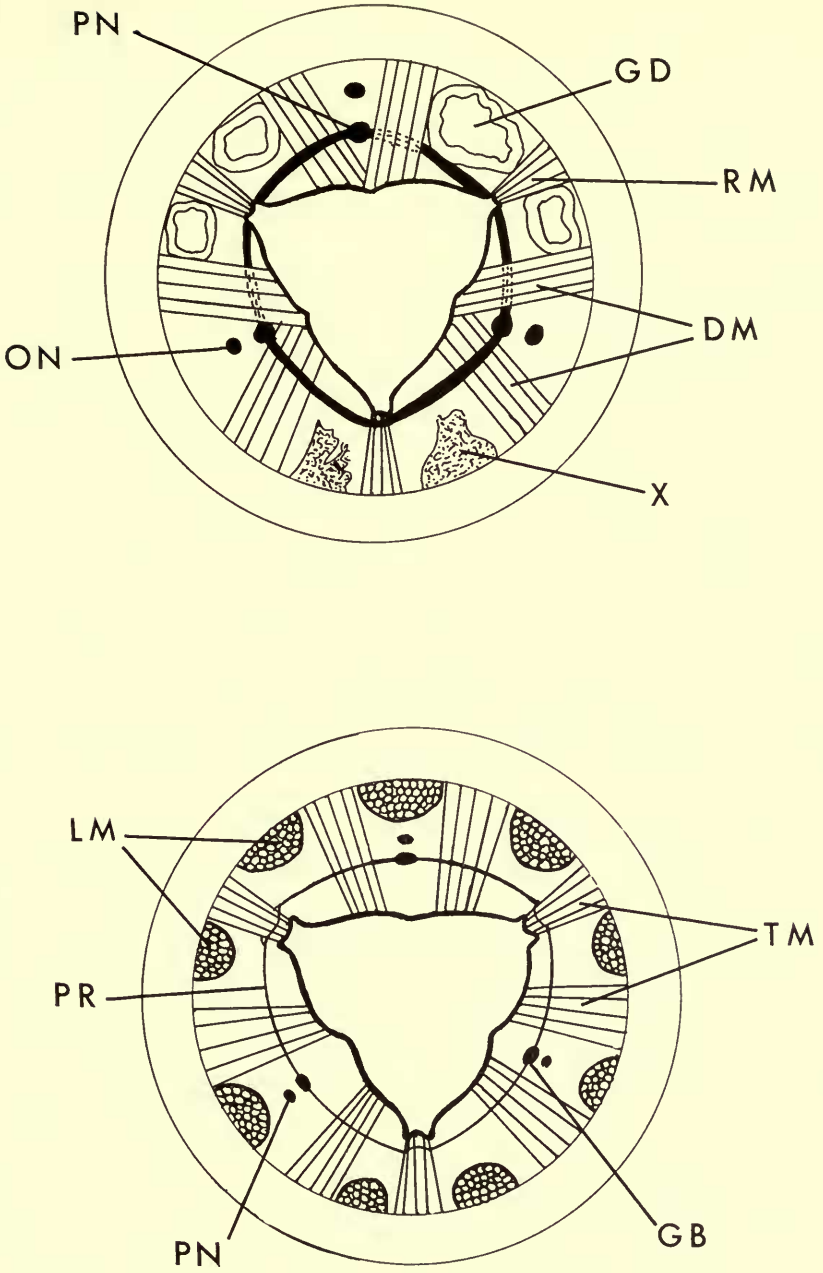

FIG. 6. Two early interpretations of the structures of the pycnogonid proboscis, as shown in transverse section. *Above :* interpretation by Dohrn (1881) of the proboscides of *Trygaeus communis* Dohrn and *Endeis spinosa* Phillippi. *Below:* interpretation by Hoek (1881) of the proboscis of *Nymphon robustum* Bell. See p. 223 for the key to the lettering.

The cross-sectional shape of this foregut lumen reflects the basic triradial symmetry of the proboscis (see above, p. 204), which arises from the fusion of a single dorsal and two ventrolateral antimeres. Thus, throughout its length the foregut is trifoliate in cross-section, although in regions of greatest cross-sectional area the shape may approach that of an equilateral triangle. For the purposes of this discussion, the ridges of the foregut (Text-fig. 7 R), which mark the boundaries between the three antimeres, are referred to as radial, while the walls between the ridges are considered to be interradial.

Throughout all the length of the foregut in the three species studied, the radial ridges are thicker than the interradial walls, but each interradial wall bears a groove (Text-fig. 7, IRG) whose floor is thickened.

In the proximal third of its length in the species so far studied, the foregut wall bears annular bands of red-staining thickened cuticle (Pl. 2, AT). These bands bear fine, long, setae which project forwards and slightly inwards, so that the entire lumen of the foregut in this region is filled with a fine meshwork (Text-fig. 7, Pl. 2, 4, 5. FS.). It appears that this structure acts both as a mechanism for macerating tissues ingested by the pycnogonids, and also as a filter, which prevents the passage of large, hard, objects into the narrow posterior end of the foregut.

While the cross-sectional area of the anterior portions of the foregut may vary differently in different species, in all the species studied so far the cross-sectional area of the foregut decreases abruptly in the proximal third of its length.

In all three species the foregut empties into the midgut through a very narrow tube which is carried well into the lumen of the midgut in a papilla (Text-figs. 4 and 5, Pl. 2 Va). It would appear that this papilla must act as a very simple non-return valve (see p. 216).

The outer wall of the proboscis and the lips.

In *P. stearnsi* and *Rh. australis* the wall of the proboscis is composed of uniformly red-staining, thick cuticle, except where the outer wall merges into the walls of the lips. In *A. glaciale* the proboscis wall is quite different in appearance. Where the proboscis is narrow and downcurved, the wall consists of a thick, non-staining, matrix of cuticle, which bears fine annular grooves set closely together at regular intervals. At the base of each groove and extending to the inner surface of the proboscis wall is a ring of cuticle which stains dark red. The muscles which produce changes in the foregut volume are all inserted into the red-staining rings. In the more proximal regions of the proboscis, the wall is uniformly red-staining and is similar in appearance to the proboscis walls of *P. stearnsi* and *Rh. australis*.

If it is accepted that the non-staining, highly refractile, cuticle is more elastic than the red-staining cuticle, then it appears that the narrow portion of the proboscis of *A. glaciale* is flexible, and that the flexibility has been achieved without any loss of efficiency of the muscles which alter the foregut volume, since these muscles are attached to highly inelastic cuticle. Conversely, the proboscides of *P. stearnsi* and *Rh. australis* are unlikely to undergo any alterations in shape.

The three lip lobes of the proboscis are more strongly developed in *P. stearnsi* and *Rh. australis* than in *A. glaciale*. In *P. stearnsi* all three lips are of approximately

equal size, whereas in *Rh. australis* the dorsal lip is much smaller than the two ventrolateral lips.

In *Rh. australis* and *P. stearnsi* the interradial portions of the end of the proboscis are composed of arthrodial membrane, while the radial ridges of the foregut are firmly anchored to the outer proboscis wall by non-staining, refractile, cuticle. At the mouth aperture itself, and for a short distance posterior to the aperture, the interradial grooves of the foregut are enormously thickened with non-staining, refractile cuticle, which is expanded backwards and outwards, into large apophyses (Text-figs. 3, 5 and 7, Pl. 3 fig. 1, ApP). To these apophyses are attached the tendons of the lip muscles (Text-fig. 7, Lpt, LpM). In *P. stearnsi* a lip apophysis occurs on each interradial groove, while in *Rh. australis* the interradial groove of the dorsal antimere is devoid of an apophysis. Of all the structures observed in the proboscides of the three species, the lip apophysis and musculature alone depart from the basic triradial symmetry.

The Intrinsic Musculature of the Proboscis.

In the three species which were the object of this study, four functionally distinct types of muscles can be seen. The muscles of all four types—and indeed all the muscles which have been observed in the Pycnogonida—are striated (Pl. 4).

The radial muscles (Text-fig. 7, Pl. 3, 4 and 5, RaM) occur throughout the entire lengths of the proboscides of the three species. They connect the thickened radial ridges of the foregut to the inner surface of the proboscis wall.

In any one plane, a pair of interradial muscles can be seen in each of the three interradii of the proboscis. These muscles are inserted immediately on either side of the thickened interradial grooves of the foregut wall, and they pass outwards to the inner surface of the proboscis wall (Text-fig. 7, Pl. 3 and 4, IRM). Dohrn (Text-fig. 6, DM) depicted the interradial muscles as overlapping in their regions of insertion on the foregut wall. This condition cannot be observed in the three species described here.

In *A. glaciale* and *Rh. australis* the radial and interradial muscles occur as numerous rings of muscles, all the components of each ring lying in the same plane, at right angles to the longitudinal axis of the proboscis. In *P. stearnsi* the interradial muscles are arranged as in the other two species, but in the proximal two thirds of the proboscis the radial muscles run oblique to the long axis of the proboscis, so that their insertions on the foregut wall lie slightly posterior to their origins on the surface of the proboscis wall.

The third type of muscle is the circular muscle (Text-fig. 7, Pl. 4, 5 CM) which occurs only in the proximal region of the foregut, where the foregut cross-sectional area decreases abruptly. Each circle of muscles consists of three arcs of fibres, which are inserted at both ends on to the thickened radial ridges of the foregut. The rings of circular muscles alternate with the rings of radial and interradial muscle fibres.

Dohrn, Hoek, Wirén (loc. cit.) all interpreted these circular muscles as nerve fibres (Text-fig. 6, PR) linking three longitudinal nerve fibres, and innervating the radial and interradial muscles. The clearly striated nature of the circular fibres,

and their insertions on the radial ridges of the foregut leave no doubt that the fibres are contractile, and not nervous, in function.

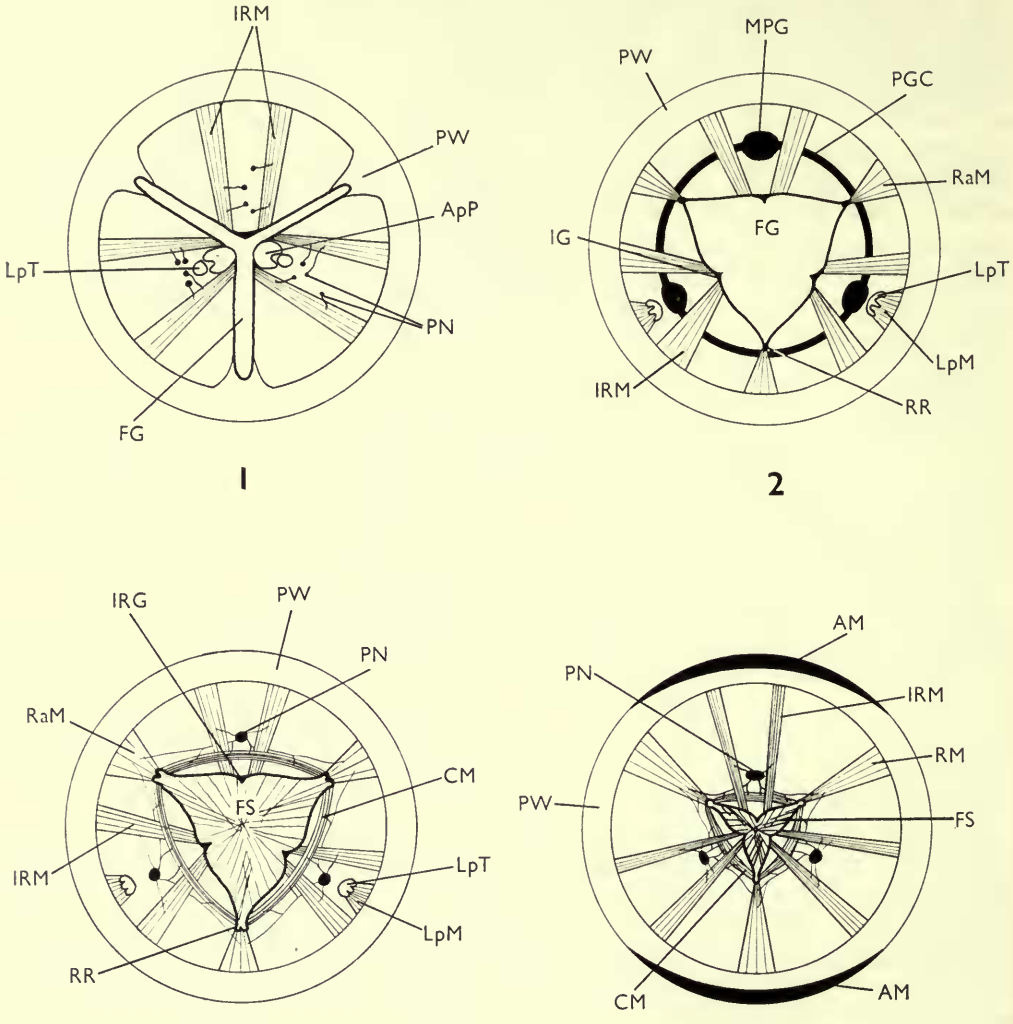

FIG. 7. Interpretation of the structures of the proboscides of *Rh. australis*, *A. glaciale* and *P. stearnsi*, as shown by transverse sections. 1. Section immediately posterior to the anterior surface of the proboscis of *Rh. australis* ; 2. Section at the level of the main proboscis ganglia, in *Rh. australis* ; 3. Section posterior to section 2, in *Rh. australis* ; 4. Section at the level of the insertion of the proboscis into the cephalic somite, in all three species. Sections 1, 2, and 3, differ from the sections at the same levels in *A. glaciale* only in the presence of lip musculature, tendons and apophysis, and from sections of *P. stearnsi* only in the absence of the dorsal lip musculature. See p. 223 for the key to the lettering.

The three longitudinal nerve fibres do exist and in most sections they lie very close to the circular muscles. However, under phase contrast illumination, fine nerves can be traced from the longitudinal nerve trunks to the radial, the interradial, and the circular muscles.

The fourth type of musculature—the lip muscles—occurs only in *P. stearnsi* and *Rh. australis* (Text-fig. 7, Pl. 3, 5 fig. 1, LpM). In both species, the muscles originate on the inner surface of the proboscis wall, and run obliquely forwards to their insertions on a tendon (Text-fig. 7, LpT) which is attached to the large lip apophyses of the two ventrolateral antimeres. In *P. stearnsi* only a third lip muscle with its tendon and lip apophysis lies in the dorsal antimere. The muscles and their tendons lie between the interradial muscles of each antimere.

Dohrn (loc. cit.) gives no indication of finding similar lip musculature in the species that he studied, but describes three sets of muscles which are apparently modified anterior interradial muscles. These muscles (" Retraktoren der Lippen ") are little longer than the normal interradial muscles. Wirén (loc. cit.) describes a similar but slightly more complicated modification of three sets of interradial muscles in *Nymphon mixtum* Kröyer.

Hoek (loc. cit.), on the other hand, describes no less than nine bundles of longitudinal muscles (Text-fig. 6, LM) in *N. robustum*, but does not indicate their sites of insertion, nor did he hazard any guesses as to their functions. Doubtless, some of the structures that he considered to be longitudinal muscles are the diverticula of the gut and the gonad which appear to extend almost to the tip of the proboscis in all pycnogonids, (Pl. 4, GND).

The Nervous system of the Proboscis.

All of the previously published descriptions of the nervous system of the proboscis have agreed on the general pattern of innervation of the muscles. Sections of *P. stearnsi*, *Rh. australis* and *A. glaciale* suggest either that the previously described species differ markedly from these three, or else that earlier authors have been misled by the original interpretation of the circular muscles as rings of nerves.

Wirén (loc. cit.) has given the most comprehensive account of the nervous system of a pycnogonid, and all subsequent descriptions have differed but little from the basic plan envisaged by him. Essentially, Wirén's description indicates three major proboscis nerves, one for each antimere. The dorsal antimere receives its major nerve from the dorsal ganglion of the brain, and each of the ventrolateral antimeres receives its major nerve from one side of the ventral ganglion of the brain. These three nerves run forward to three large proboscis ganglia, situated just behind the tip of the proboscis, which are linked by circular fibres. Nerves run forward from the proboscis ganglia to a group of three small ganglia in each antimere. Wirén considered that these small ganglia, which are all interconnected, control the movement of the lips. From the three main proboscis ganglia there run backwards, inside the main proboscis nerves, three nerve trunks which are linked, at regular intervals, by circular nerve fibres. Small nerves from these circular fibres run to the radial and interradial muscles. Wirén depicts the circular nerve fibres in the proximal portion of the proboscis only, and as he described no other circular strands

in the proboscis, and as the radial and interradial muscles occur throughout the whole length of the proboscis, it seems highly likely that his " circular nerve fibres " are, in fact, the circular muscle fibres which are so clearly distinguishable in the three species discussed here.

In all three species there are three main nerve trunks, with origins and positions similar to those depicted by Wirén. These three main nerves terminate in ganglia situated well behind the tip of the proboscis ; the ganglia are joined by arcs of stout nerve fibres. There are, however, no smaller lip ganglia anterior to the main ganglia. This is not surprising, since in *A. glaciale* there are no special lip muscles, while in *P. stearnsi* and *Rh. australis* the major part of the lip musculature lies posterior to the main ganglia. In the latter two species, a group of fine nerves runs back from the main ganglia above the main proboscis nerves, and gives off branches to the lip muscles.

Posterior to the main proboscis ganglia each main proboscis nerve consists of a group of fine fibres, rather than a single nerve trunk, although in places these fibres form a bundle. From the fibres, very fine nerves can be traced, running to the radial, the interradial, and—in the most proximal region of the proboscis–the circular muscles.

Methods of functioning of the proboscis.

It appears that the elasticity of the foregut wall is the major antagonist of the radial and the interradial muscles.

Contraction of the interradial muscles will cause the interradial walls of the foregut to be pulled towards the wall of the proboscis. The force applied by the interradial muscles will produce tension forces in the thickened floor of each interradial groove, and also tension forces in the thickened radial ridges. Contraction of the radial muscles, at the same time as the interradial muscles, will produce additional tension forces in both the interradial grooves and radial ridges. The radial muscles act, at the same time, as struts by which the whole foregut is kept in constant position within the proboscis lumen.

The overall result of the contraction of these two sets of muscles will be to change the cross-sectional shape of the foregut from trifoliate to more nearly triangular. As the foregut cross-sectional shape changes, so the volume of the foregut will increase. The lowering of pressure of the foregut lumen will produce an inrush of material from outside the animal, when the lips are open.

Relaxation of the radial and interradial muscles will release the tension forces engendered in the foregut grooves and ridges. These forces will tend to return the foregut to its original, trifoliate, cross-sectional shape. The volume of the trifoliate section foregut is less than when the foregut is triangular in section, and therefore the pressure of the foregut contents will rise when the tension forces in the foregut walls are released. If the lips are securely closed, and the rings of radial and interradial muscles relaxed, the foregut contents will be forced backwards.

However, the foregut cross-sectional area decreases markedly along the proximal third of its length, and strong frictional resistance will be engendered by the backward passage of material through this region. Resistance to movement of gut

contents will be further increased in the proximal regions of the proboscis by the dense filter of setae projecting into the lumen.

However, it is along the proximal third of the length of the foregut that the circular muscles occur. The antagonist of these muscles is the chitinous foregut wall, which is here greatly reinforced by thick annular bands, bearing the setae which form the dense filter. Alternate contraction and relaxation of the radial and interradial muscles in this region will produce variations in the cross-sectional area of the foregut. Reduction of cross-sectional area of the foregut, following relaxation of the radial and interradial muscles, will be further assisted by contraction of the circular muscles.

The movements of the foregut wall will cause movements of the setae forming the filter. When the foregut contents anterior to the filter are under pressure, this movement of the setae will result in the food material being gradually pushed backwards through the filter and eventually into the midgut, being finely macerated as it moves through the filter.

It does not appear possible for the haemocoelic and other fluid spaces in the pycnogonids to act as the antagonists of the radial and interradial muscles and the mechanism described above would work equally well if the body fluids were not of fixed volume. It does appear likely, however, that hydrostatic pressure of the body fluids does play a part in ensuring the closure of the mouth.

When the volume of the foregut increases, the hydrostatic pressure of all the body fluids will be increased, as there is no separation of proboscis and trunk haemocoelic spaces. This rise of pressure will tend to force the proboscis forward, further into the material which it is ingesting. The hydrostatic pressure of the body spaces will remain high, even when food is being pushed backwards into the midgut. Thus when the lip musculature is relaxed, and the food is being forced back into the midgut, the tip of the proboscis will remain pushed into the food material. The only process which will lower the animals' internal pressure after food has been ingested is the evacuation of faeces from the hindgut.

The opening and closing of the lips is readily understood if the degree and distribution of sclerotization of the end of the proboscis is borne in mind. The interradial lip apophyses (ApP) are connected with the highly sclerotized proboscis wall by a region of arthrodial membrane. When tension is applied to the lip tendons, by contraction of the lip muscles, the interradial walls of the foregut will be pulled backwards and upwards, and the mouth opened. Closure of the mouth is achieved by the release of tension forces engendered in the enormously thickened interradial grooves of the lips during the opening of the mouth.

MORPHOLOGICAL ADAPTATIONS TO PREFERRED FOOD MATERIALS

The clear preference shown by *A. glaciale* for a single species of polyzoan, *Cellarinella foveolata* (Waters) (Br 3), can be interpreted readily in terms of the functional anatomy of the pycnogonid and the polyzoan. *A. glaciale* is obviously highly adapted to feeding on this particular form of polyzoan.

Two sets of characters of the polyzoan zooecia and colonies appear to be critical in determining whether or not a particular species of polyzoan is available to *A.*

glaciale as food. These are (a) the presence or absence of frontal wall pores, and their diameters, and (b) the shape, size and strength of the polyzoan colonies.

It seems highly unlikely that *A. glaciale* is capable of piercing the frontal wall of a zooecium, even if a zooecium is not heavily chitinised or calcified. Penetration to the polypide through the operculum is fraught with danger. Even if the pycnogonid were able to place its proboscis in the orifice, the closing operculum, which is usually very thick, would probably crush it. Furthermore, the polyzoan orifice may be screened by an avicularium. The movable jaw of the avicularia in *Camptoplites bicornis* (Br 4) and *Notoplites drygalski* (Br 2) is as much as 0·08 mm. in diameter, and could doubtless inflict considerable damage on the pycnogonid proboscis should the proboscis lie within the jaws during one of their sporadic closures.

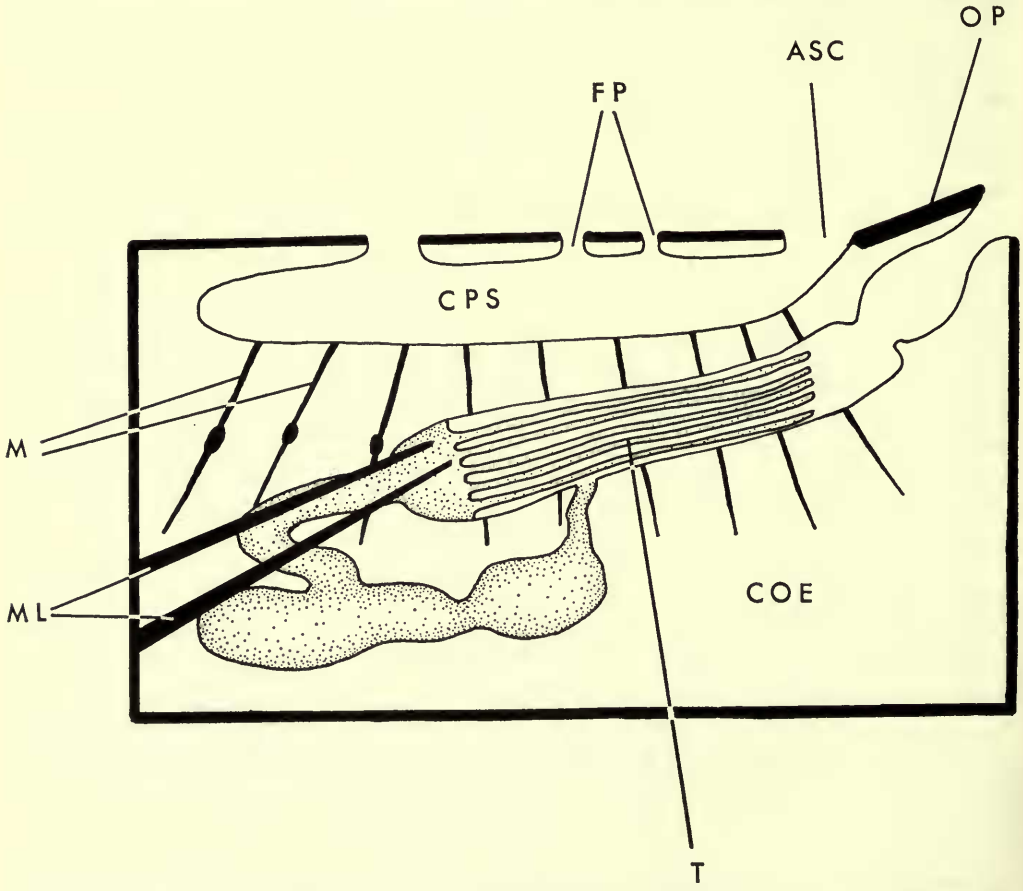

FIG. 8. Diagrammatic longitudinal optical section of the zooecium of *Cellarinella foveolata* (Waters) (Polyzoa Ectoprocta Ascophora), showing the structures which bring about the protrusion and retraction of the lophophore. See p. 223 for the key to the lettering.

It would appear that the fine distal portion of the proboscis is used to probe through the frontal wall pores of the zooecium, through the compensation sac, and

into the coelom of the polypide. The frontal wall pores are rarely straight tubes, and the flexibility of the distal portion of the proboscis, which will allow it to traverse an irregular tube, is an obvious advantage to the pycnogonid. The disposition and size of the M 2 extrinsic muscles suggests that the tip of the proboscis can be pressed downwards with considerable force. Such force must be required to rupture the walls of the compensation sac and gain access to the coelom of the polypide.

A considerable advantage to the pycnogonid of piercing the compensation sac is that the tentacles of the polypide cannot be extruded once the compensation sac is ruptured (see Text-fig. 8). Presumably the polypide will retract as the pycnogonid investigates the frontal wall of the zooecium with its palps, and then begins to probe the frontal pores. Once the compensation sac has been punctured the pycnogonid can feed at leisure on the entire polypide.

The adults of *A. glaciale* have a leg span of approximately 10 mm. If a polyzoan colony has a width or circumference of very much less than 10 mm. the pycnogonid will be unable to anchor itself firmly while thrusting downwards with its proboscis. Alternatively, a widely spread colony of many fine branches with rigid nodes will provide as firm a platform upon which the animals can cling and feed as will a single firm, stout, branch.

TABLE IV

Br 1. *Cellarinella laytoni*
Shape : Cylindrical
Diameter : 0·8 to 2·0 mm.
Branches : Firm
Frontal Pores : Present, av. diam. 0·06 mm.

Br 2a. *Escharoides bubeccata*
Shape : Cylindrical
Diameter : av. 1·15 mm.
Branches : Firm
Frontal Pores : v. few, peripheral, partly concealed, av. diam. 0·04 mm.

Br 2b. *Notoplites drygalski*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Flexible
Frontal Pores : Absent

Br 3. *Cellarinella foveolata*
Shape : Broad and Flat
Width : 2 to 40 mm.
Colony : Firm
Frontal Pores : Numerous, diam. 0·02 to 0·12 mm.

Br 4a. *Camptoplites bicornis*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Flexible
Frontal Pores : Absent

Br 4b. *Cellarinella wandeli*
Shape : Cylindrical
Diameter : 0·6 to 0·9 mm.
Branches : Firm
Frontal Pores : Absent

Br 5a. *Cellaria vitrimuralis*
Shape : Cylindrical
Diameter : av. 0·75 mm.
Branches : Firm
Frontal Pores : Absent

Br 5b. *Cellaria moniliorata*
Shape : Cylindrical
Diameter : 0·3 to 0·5 mm.
Branches : Firm
Frontal Pores : Absent

The distribution of the two sets of characters amongst the eight species of Polyzoa concerned in the study is shown in Table IV. Amongst the eight species, only *Cellarinella foveolata* (Br 3) fulfills the conditions of a broad, firm, colony, whose frontal walls bear large numbers of pores of sufficiently large diameter to allow easy access for the proboscis of *A. glaciale* to the underlying polypide.

Pycnogonids have been reported as associating with specimens of virtually all of the phyla whose representatives occur in the sea (see Helfer & Schlottke 1935, pp.

198–201), and the main food source of at least twenty species of pycnogonids is known with some certainty. The food of these species is, variously, Hydrozoa, Scyphozoa, Actinozoa, nudibranchs, polychaetes, holothuria, and lamellibranch molluscs. While Dohrn (1881), Prell (1910), and Helfer (1909), have reported the spatial association of *Ascorhynchus arenicola* (Dohrn), *Phoxichilidium femoratum* Rathke, and *Anoplodactylus petiolatus* Krøyer with species of ectoproct Polyzoa, *A. glaciale* is the first species which can be said, with any confidence, to actually rely on Polyzoa for its main source of food.

It is unlikely that the universally slow-moving Pycnogonida would be capable of feeding solely on the retractable lophophores of polyzoans, and we would expect to find, in any other pycnogonids feeding mainly on Polyzoa, the same slim terminal portion of the proboscis as occurs in *A. glaciale*. With this in mind, it is reasonable to suppose that species of *Pantopipetta* Stock 1963 (= *Pipetta* Loman) are predators of Polyzoa. All the species of *Pantopipetta* occur in deep water, and their faunal associations—let alone their feeding behaviour—have never been described.

One species in the genus *Ammothea* Leach possesses the necessary modification of the proboscis for feeding on Polyzoa. This is *Ammothea stylirostris* Gordon. As the specific epithet implies, the proboscis is long in this species, and tapers to a small distal diameter. In the recently discovered juvenile of this species (Hedgpeth and Fry, in preparation) the proboscis is greatly elongated, and is drawn out to a minute terminal diameter. However, the palps are much shorter than the proboscis, and clearly in evolutionary process of atrophying. It is difficult to envisage the efficient use of a very long proboscis in probing small frontal pores, if the surface to be probed cannot be explored previously by the palps.

At least nineteen species of *Austrodecus* have been described, and in all but two the proboscis is long and styliform. In *A. frigorifugum* Stock the proboscis, while still of relatively small terminal diameter, is short, and bears a small distal bulb. In *A. breviceps* Gordon the proboscis is styliform, but is relatively very short. Amongst the other species there is some variation in the degree of curvature of the proboscis, and the ocular tubercle, which presumably provides the origins of the M 2 muscles throughout the genus, varies greatly in its height. It may well be that these variations of proboscis and ocular tubercle are closely correlated with the morphology of the various Polyzoa upon which the species feed.

The marked preference shown by *Rh. australis* for *Eudendrium tottoni* (Hy 1) amongst the Hydrozoa, is readily explicable. Of the four species of Hydroidea presented to the pycnogonids, *E. tottoni* alone is athecate. Whilst the hydrothecae of *Symplectoscyphus epizooticus* (Hy 2), *S. vanhoeffeni* (Hy 3), and *Hydrodendron arborea* (Hy 6) are sufficiently wide to allow the proboscis of *Rh. australis* easy access to contracted hydranths (see Totton 1930), the hydranths of *E. tottoni*, which cannot be withdrawn into a protective cup, will be discovered far more readily by accidental contact.

There is no obvious reason why the two species of Alcyonaria should occupy so low a position in the food preferences of *Rh. australis*, unless the nematocysts of *Thouarella variabilis* (Hy 4) and *Alcyonium paessleri* (Hy 5) are capable of penetrating the

exoskeleton of the pycnogonid. Nematocysts do not deter various species of *Pycnogonum* from feeding on Actinia (Sars 1881, Mobius 1893, Prell 1910, Loman 1925, 1928, Stephenson 1933, Zeigler 1960, et al.). However, the Actinian organization, and the pattern of development of nematocysts, is such that by feeding at the base of the column the pycnogonids can avoid contact with functional nematocysts It is unlikely that *Rh. australis* could feed on either of the species of Alcyonaria without coming into contact with the hydranth nematocysts.

A far more likely explanation of a low preference for the alcyonarians is the fact that *Rh. australis* is not likely to encounter *Th. variabilis* or *A. paessleri* as frequently as it does the hydroids. In contrast to the hydroids, which grow in and on the surface of the substrate, the two alcyonarians are erect in form, and usually rise several centimetres above the surface of the substrate (see Bullivant 1959b, 1961). *Rh. australis* was always found either within the sponge spicule mat or at its surface

On the other hand, several large specimens of *Nymphon australe* Hodgson were taken on colonies of both species of Alcyonaria, and climbed on and clung to fragments of the alcyonarians kept in an aquarium in the laboratory.

As was stated above, there can be little doubt that the major food source of *P. stearnsi* is actinians, although small individuals are taken from amongst large hydroids. All told, approximately thirty species of Hydrozoa and Anthozoa are known to be either the food, the site of larval development, or at least the preferred substrate of fifteen species of pycnogonids. In all of these pycnogonid species the proboscis is bluntly rounded terminally and is of relatively large and uniform diameter throughout its length. Such a proboscis shape appears to be ideally suited for the ingestion of large pieces of soft coelenterate tissue. Since the tissues of the prey are relatively soft, the pycnogonids have no need for mechanisms for piercing or pushing hard against the prey. On the other hand the ingestion of large morsels of food requires that the mouth can be opened wide. It has been shown (above) that the lip opening musculature of *P. stearnsi* is more highly developed than that of *Rh. australis*.

The significance of the secondary bilateral symmetry of the lip musculature in *Rh. australis* is not readily apparent. Presumably this condition represents an adaption for preventing the mouth from opening widely, and it appears to be a very crude solution to such a need, unless the innervation of the lip musculature in Pycnogonida does not allow for partial opening or closing of the mouth [In other words, nervous stimulation of the lip muscles results only in all the muscle fibres being either fully contracted or fully relaxed]. It is an obvious advantage to the pycnogonid, which ingests food by suction, that the size of the mouth aperture should be closely related to the size of the food morsels to be ingested. *Rh. australis* and *P. stearnsi* must be able to generate enough suction to tear portions of hydrozoan tissue from their parent body. However great the suction power which can be generated, little tissue will be detached and ingested if sea water can enter the proboscis around the food material.

P. stearnsi inserts its proboscis deeply into a thick wall of anemone tissue, and therefore can ingest food through a very wide aperture. *Rh. australis*, on the other

hand, must attach the tip of its proboscis, by suction, to a relatively very small hydroid polyp, which it must tear from the colony by suction. It can only do this efficiently if the mouth gape is always smaller than the polyps upon which it feeds.

This reduction of the mouth gape in *Rh. australis* does not appear to be an adaption for feeding solely on *E. tottoni* (Hy 1), but rather for feeding on any hydroids with small polyps, for all of the hydroids encountered in the environment have polyps of very similar dimensions (see Totton, loc. cit.).

The preferred foods of the two other species of *Rhynchothorax—Rh. mediterraneus* Costa and *Rh. philopsammum* Hedgpeth—are totally unknown. The proboscis of all three species are of similar size and shape, indicating ingestion of relatively large food particles.

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KEY TO LETTERING IN TEXT-FIGURES AND PLATES

AM	Arthrodial membrane
ApP	Interradial lip apophysis
Ap 1, 2	Apophyses
ASC	Ascopore of the compensation sac
AT	Annular sclerotization
CM	Circular muscles
COE	Coelom of polypide
CPS	Compensation sac
DG	Dorsal ganglion of the brain
1 DL	1st major midgut diverticulum
2 DL	2nd major midgut diverticulum
DM	Dilator muscles
FG	Foregut
FP	Frontal pores of compensation sac
FS	Filter of setae borne on annular sclerotizations
GB	Ganglionic bundle
GND	Gonad
IG	Interradial grooves of foregut
IRM	Interradial muscles
LM	Longitudinal muscle bundles
LpM	Lip muscles
LpT	Lip tendon
M	Muscles producing inflation of the compensation sac
MG	Midgut
ML	Muscles retracting the lophophore
MPG	Main proboscis ganglion
M1–3	Extrinsic proboscis muscles
M4, 5	Intersegmental muscles
ON	Outer nerve
OP	Operculum
OT	Ocular tubercle
P	Proboscis
PGC	Proboscideal ganglionic commissure
PN	Proboscis nerve
PW	Proboscis wall
RaM	Radial muscles
RM	Retractor muscles
RR	Radial ridges of the foregut
T	Retracted tentacles
TM	Transverse muscles
Va	Valve between foregut and midgut
VG	Ventral ganglion of brain
X	Tissues of unknown function

PLATE 1

Longitudinal vertical section of the anterior portion of the trunk, and the base of the proboscis, of *A. glaciale*.

See p. 223 for the key to the lettering.

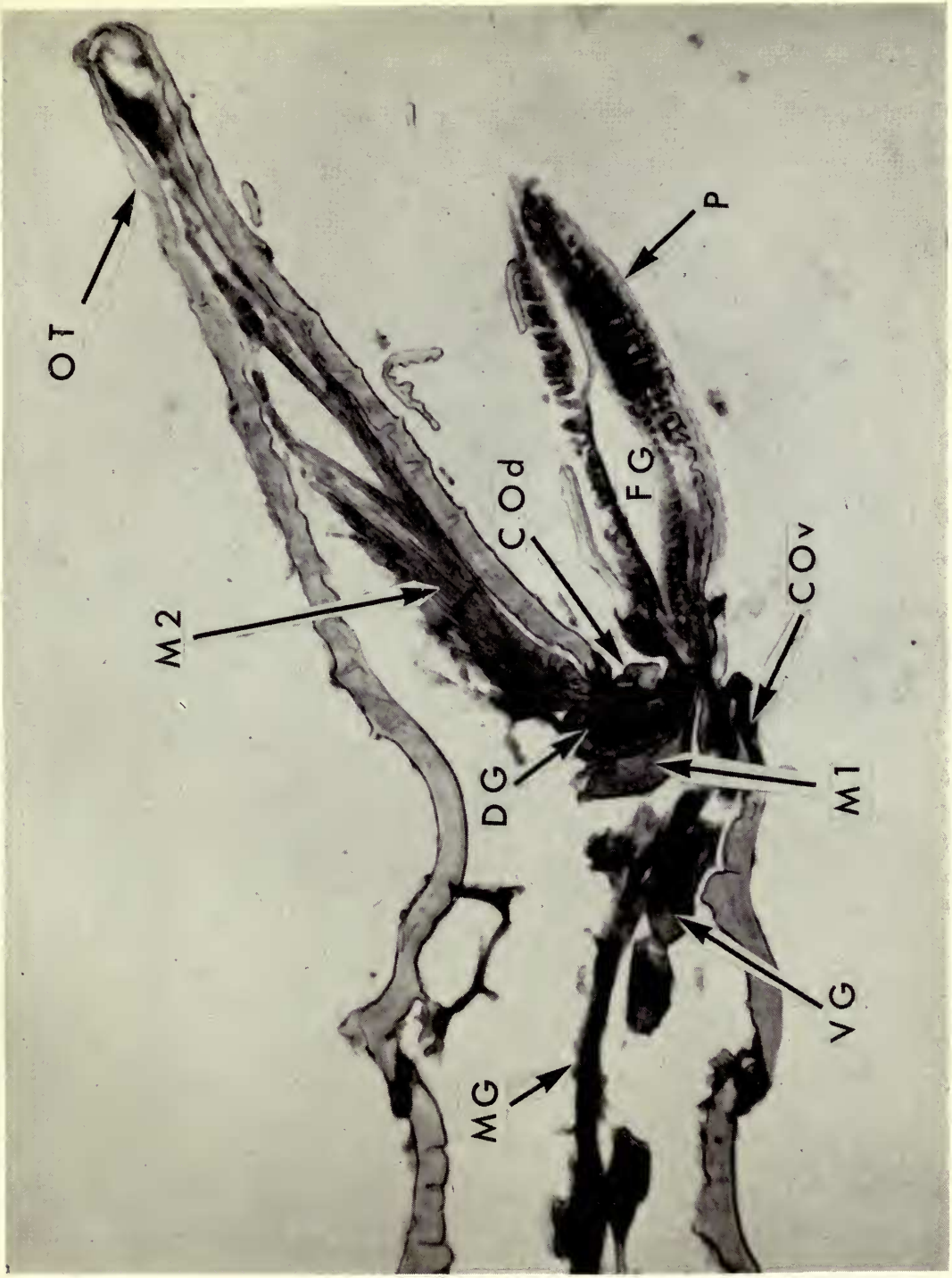

OT
M2
COd
FG
P
COv
DG
M1
MG
VG

PLATE 2

Longitudinal vertical section of the cephalic somite, and the base of the proboscis, of *P. stearnsi*.

See p. 223 for the key to the lettering.

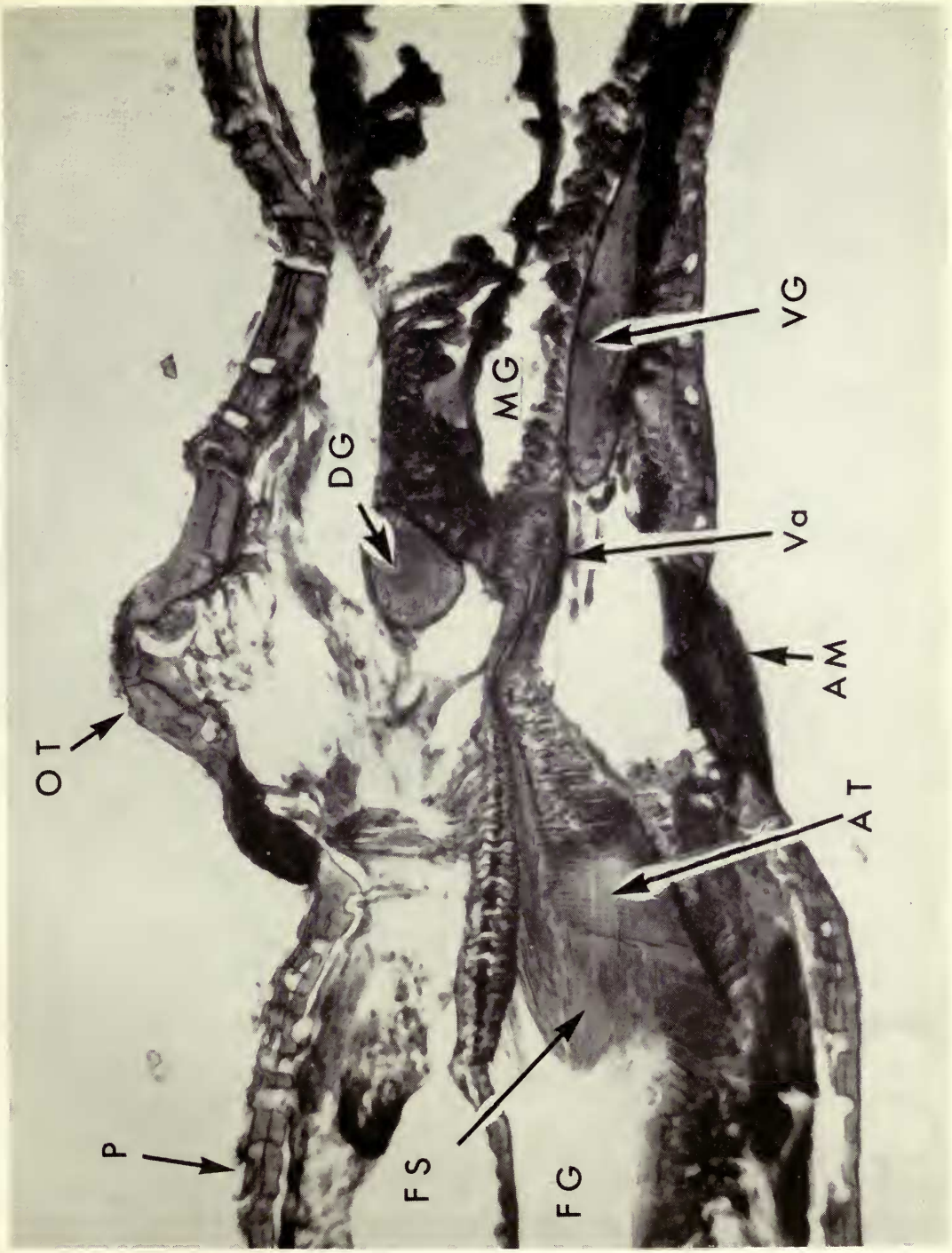
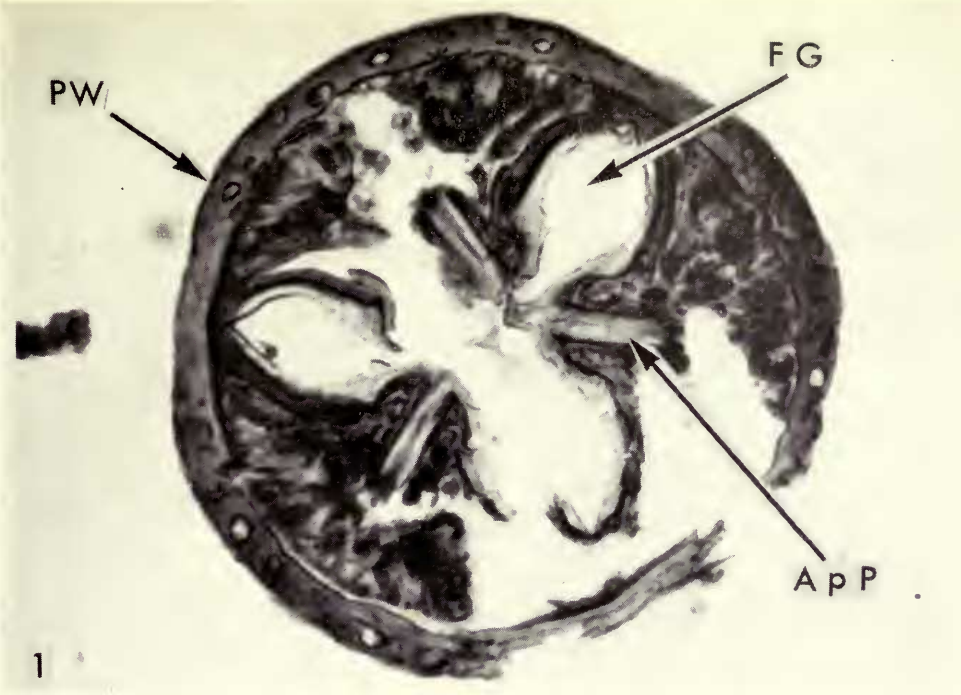

P
OT
DG
MG
VG
Va
AM
AT
FS
FG

PLATE 3

Transverse sections of the proboscis of *P. stearnsi*. (Upper) in a plane immediately posterior to the tip of the proboscis ; (Lower) posterior to (Upper) at the level of the main proboscis ganglia.

See p. 223 for the key to the lettering.


PW
FG
ApP
1

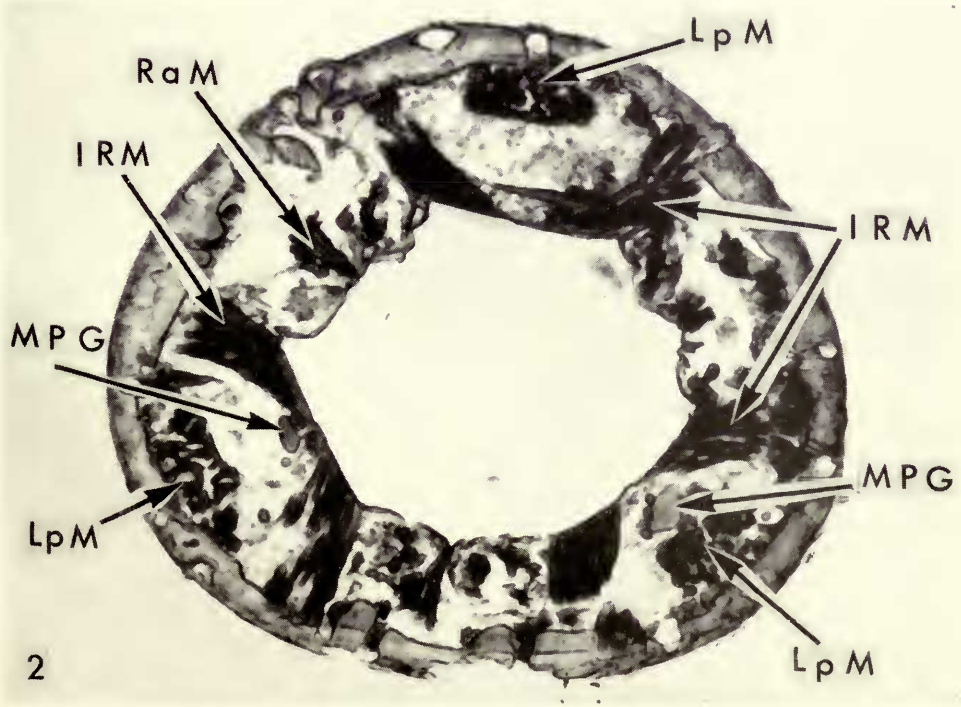
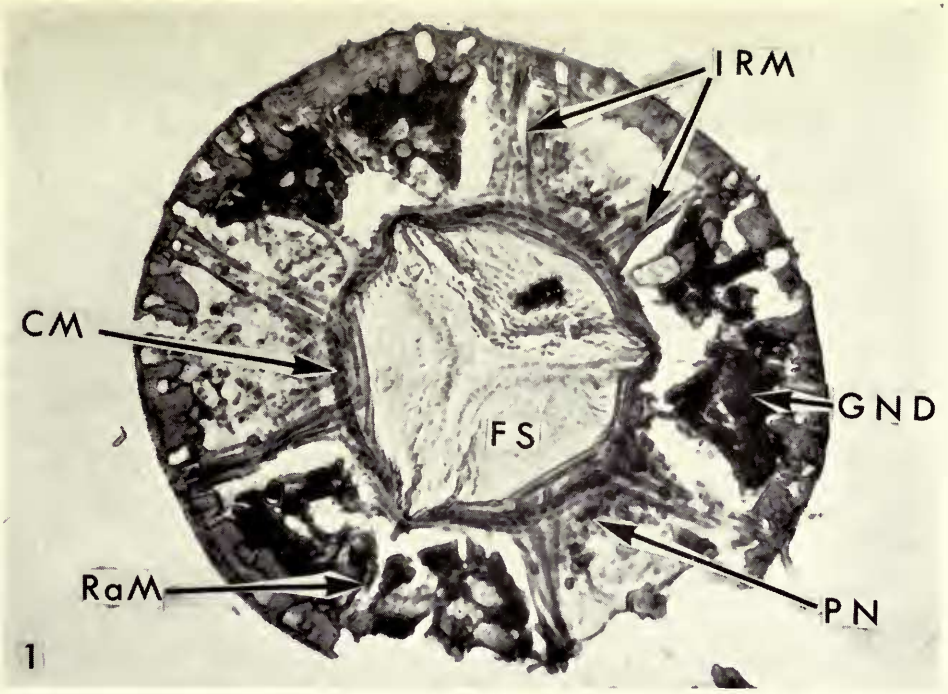

LpM
RaM
IRM
IRM
MPG
MPG
LpM
LpM
2

PLATE 4

Transverse sections of the proboscis of *P. stearnsi*, at levels posterior to those shown in Pl. 3. (Upper) through the proximal third of the proboscis ; (Lower) at a plane immediately anterior to the insertion of the proboscis into the cephalic somite.

See p. 223 for the key to the lettering.


IRM
CM
GND
FS
RaM
PN
1

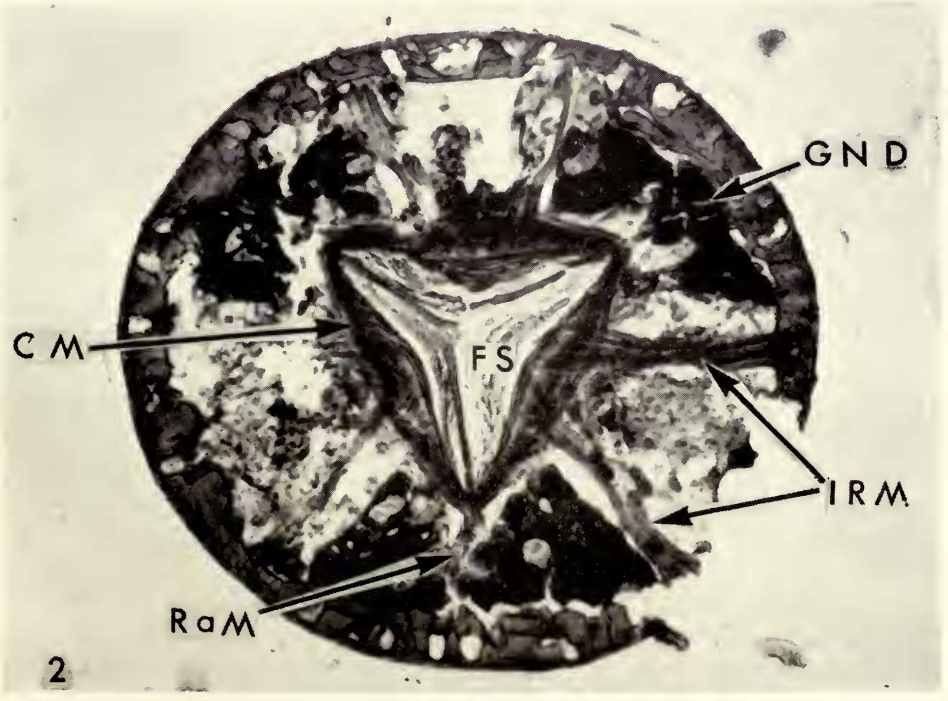
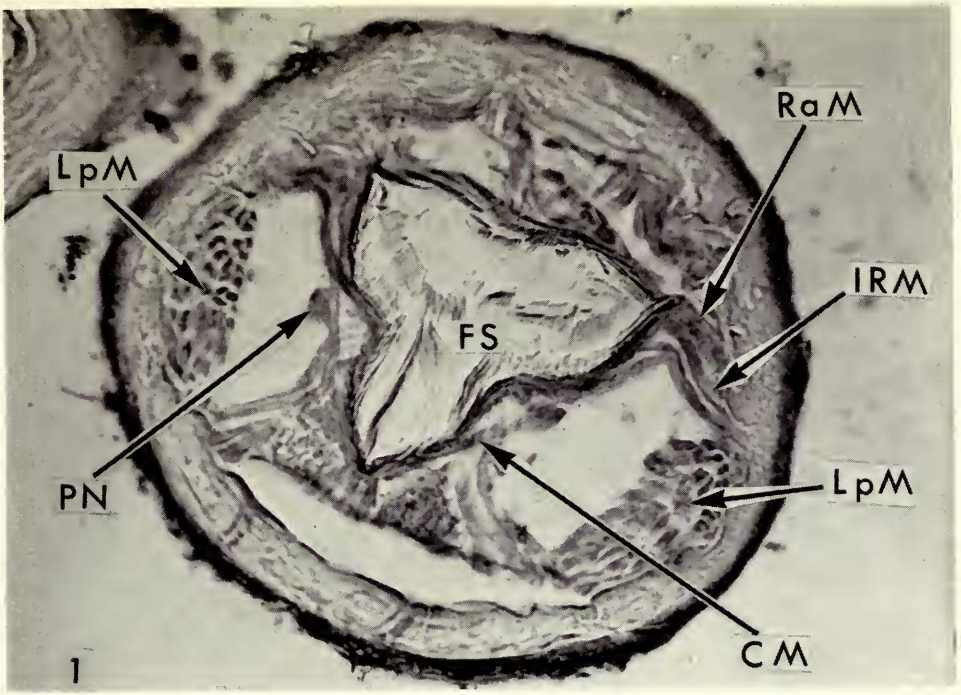
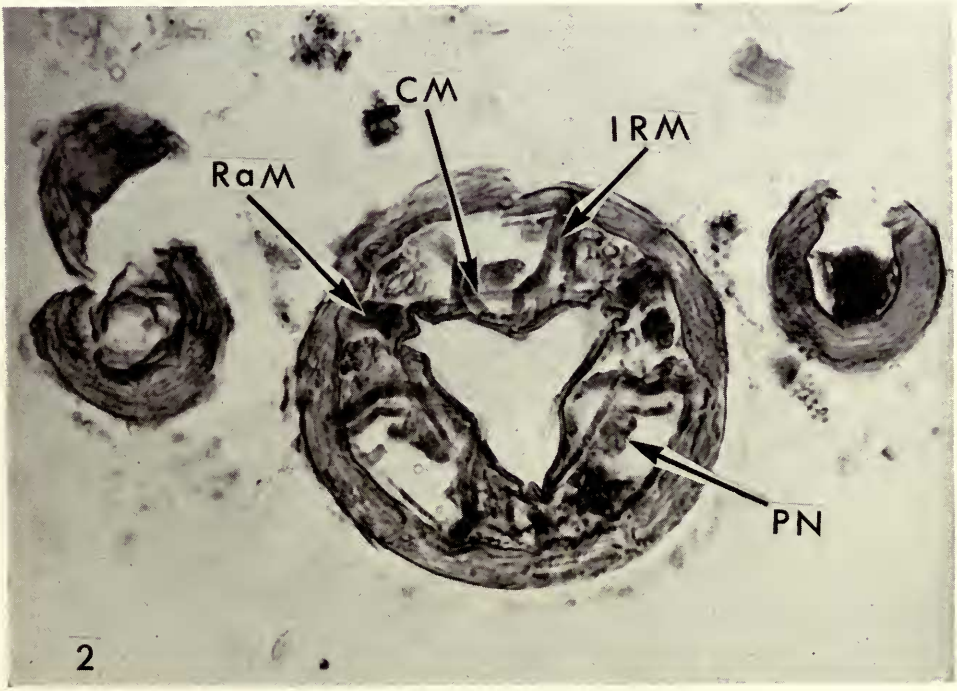

GND
CM
FS
IRM
RaM
2

PLATE 5

(Upper) transverse section of the proboscis of *Rh. australis*, slightly posterior to the midpoint of the proboscis length, showing the presence of lip musculature in the two ventrolateral antimeres only ; (Lower) transverse section through the proximal third of the proboscis of *A. glaciale*.


RaM
LpM
IRM
FS
PN
LpM
CM
1


CM
IRM
RaM
PN
2